Long-term change in bioconstruction potential of Maldivian coral reefs following extreme climate anomalies

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Abstract

Global climate change has increased the frequency and intensity of extreme heat anomalies and consequent mass coral bleaching events. Long term dynamics of hard coral cover, bioconstruction potential, carbonate deposition, and reef accretion were monitored over a 20-year period on Maldivian coral reefs in order to investigate the effects of high-temperature anomalies on coral reef accretion and their recovery potential. Changes experienced by shallow reefs between 1997 and 2017 were evaluated by considering five different bioconstructional guilds and the BioConstruction Potential index (BCP), a proxy for the constructional capacity of reefs. Abnormally high temperatures in 1998 and 2016 led to severe coral bleaching and consequent mortality, especially of the primary builders. Renewed carbonate deposition was not documented until 2-3 years after the bleaching, and 6-9 years passed until constratal (i.e., low relief) growth was achieved. Finally, 14-16 years were required to reach accretion rates high enough to ensure superstratal (i.e., high relief) growth. Coral mortality in the Maldives during the 2016 bleaching event was lower than in 1998, and the initial recovery was faster and occurred via a different trajectory than in 1998. Rising levels of anthropogenic carbon emissions are predicted to accelerate sea level rise and trigger severe coral bleaching events at least twice per decade, a frequency that will 1) prevent coral recovery, 2) nullify reef accretion, and, consequently 3) result in the drowning of Maldivian reefs under the worst climate projections.

Introduction

Coral reefs are ecologically and economically important ecosystems that host ca. 35% of all species living in the oceans, and support the livelihood of an estimated half billion people globally, typically through fishing and tourism (Knowlton et al. 2010). These "rainforests of the sea" protect shores from storms and coastal settlements from flooding and erosion (Harris et al. 2018), and provide social, economic and cultural services with an estimated value of over USD $1 trillion globally (Heron et al. 2017 and references therein). Coral reefs result from the dynamic equilibrium between bioconstruction and erosion (Glynn and Manzello 2015). Bioconstruction is predominantly undertaken by hermatypic scleractinian corals, though coralline algae are additional contributors; collectively, these major framework builders of shallow-water tropical coral reefs deposit a calcium carbonate ($CaCO_3$) structure that persists after their death (Hamylton et al. 2017). The carbonate budget has often been identified as a key metric for assessing reef health, as it is indicative of the capacity of reefs to maintain physical 3-dimensional structures and vertical accretion (Januchowski-Hartley et al. 2017; Perry and Morgan 2017a). Mass mortality of bioconstructors following major disturbances may stop or hamper the process of bioconstruction and facilitate erosion of carbonate structures (Bianchi 2001).

Reef accretion results from vertical growth of the coral-algal framework and is mainly controlled by the rate of sea level rise (Grigg 1998). "Keep-up" reefs are typically observed as shallow, frame-building communities because their accretion rate tracks sea level rise. "Catch-up" reefs begin as shallow reefs, become deeper as the rate of sea level rise exceeds the accretion rate, but then grow upwards to avoid drowning. "Give-up" reefs are those that drowned because the accretion rates lagged behind the rate of sea level rise (Neumann and Macintyre 1985). From a geological point of view, a reef dies when its rate of accretion becomes lower than its rate of erosion, so that it cannot match the rate of sea level rise (Riegl 2001; Perry and Smithers 2010).

According to their accretion rate, reefs can develop following two main mechanisms (Gili et al. 1995): i) superstratal growth, where reef builders collectively project decimetres to metres above the substratum creating a topographic high relief; or ii) constratal growth, where vertical accretion occurs at a similar rate to sediment accumulation, so that reef relief is low, projecting centimetres only above the substratum. The ability to exhibit superstratal growth depends on the abundance of individual taxa, types of growth forms (branching corals contributing mainly) and colony size. On the contrary, constratal framework development is promoted by an abundance of encrusting organisms and secondary frame-builders (Insalaco 1998).

Global increases in seawater temperature have triggered extensive coral bleaching and mass mortality events across most tropical regions (Baker et al. 2008). Bleaching is a stress response that implies the loss of photosynthetically active dinoflagellate algae (zooxanthellae) from their hermatypic coral hosts and results in reduced calcium carbonate accretion (Gates et al. 1992; Wooldridge 2017). While corals can recover from moderate bleaching, severe or prolonged bleaching is often lethal. Anthropogenic carbon emissions have caused a 1°C increase in global surface temperature since pre-industrial times (Hoegh-Guldberg et al. 2007), which increased the likelihood of bleaching events (Baird and Marshall 2002). Thermal stress on corals has also been magnified by strong ENSO (El Niño - Southern Oscillation) events (Glynn and De Weerdt 1991; Brown et al. 2013).

Bleaching episodes worldwide have resulted in catastrophic losses of coral cover and have changed coral community composition and structure, thus leading to decline in biodiversity (Baker et al. 2008; Richardson et al. 2018). High-temperature events have increased in frequency, severity and geographic extent since the 1980s (Heron et al. 2016; Hughes et al. 2018) and three pan-tropical global bleaching episodes affected virtually all reefs in the world, in 1997-1998, 2010 and 2014-2016. The 1997-1998 El Niño devastated reefs throughout the Indian Ocean (Plass-Johnson et al. 2015; Donner et al. 2017). The Maldives were among the most affected countries, with 60-100%

coral mortality reported, depending on species and locality (Bianchi et al. 2006). The 2010 bleaching event spanned from the western Indian Ocean to the Caribbean and was particularly devastating in Southeast Asia (Guest et al. 2012; Alemu and Clement 2014), but not in the Maldives (Morri et al. 2015). Beginning in the middle of 2014, water temperatures rose enough to trigger wide-scale bleaching in the Atlantic, Pacific, and Indian oceans, which continued into 2015 and extended to the southern hemisphere in 2016 (Eakin et al. 2016). The 2014-2016 El Niño heating event was unprecedented in duration and magnitude (hottest temperatures on record); 72% of the World Heritage-listed reefs bleached (Heron et al. 2017). Coral mortality has been among the worst ever observed (Hughes et al. 2017b), and even remote and pristine reefs that experience minimal human degradation were severely affected (Hughes et al. 2017a). Also the Maldives have been hugely impacted during this third global bleaching event (Muir et al. 2017; Perry and Morgan 2017b).

Long-term monitoring studies are necessary to understand trends in marine ecosystems and their response to human disturbances (Ellingsen et al. 2017; Gatti et al. 2017). Historical data series are essential for defining recovery rates and providing baselines against which change can be assessed (Edmunds and Elahi 2007; Mumby et al. 2007; Gatti et al. 2015; Januchowski-Hartley et al. 2017; Osborne et al. 2017; Porter and Schleyer 2017). Unfortunately, uninterrupted, decadal-scale datasets are rare for marine ecosystems, making it difficult to determine the extent and rate at which global climate change is currently impacting the world’s oceans. This study analyzes a 20-year coral reef data series (1997-2017) in the Maldives, encompassing the three El Niño events in 1998, 2010 and 2016. Since 1997, annual investigations of coral reef state have been conducted during April-May (Bianchi et al. 2009). This allows us to compare the state of coral reefs before, during and after these bleaching events and document subsequent recovery.

The main aims of this study were to i) compare the three bleaching events in terms of coral mortality and recovery, ii) investigate relationships between reef bioconstruction potential (measured using the recently proposed BioConstruction Potential index BCP (Bianchi et al. 2017), carbonate deposition and reef accretion to make conjectures about the capacity of Maldivian reefs to cope with sea level rise, and iii) explore the relationship between bioconstructor diversity and reef accretion.

Materials and methods

Study area and field activity

The Maldives, comprised of 27 atolls and ca. 1120 islands, form the central part of the Laccadive-Maldives-Chagos ridge in the central Indian Ocean, stretching in a north-south direction from about 7°07’ N to 0°40’ S in latitude and 72°33’ E to 73°45’ E in longitude.

Between 1997 and 2017, scientific cruises took place in April-May of each year, when eight sites were surveyed across the atolls of Ari, Felidhoo, Gaafu Alifu (Suvadiva), North Malé, South Malé, Rasdhoo, Thoddoo. Four were ocean reef sites, i.e. ocean-facing sides (fore reefs) of the atoll rims, and four were lagoon reef sites, i.e. lagoon patch reefs or lagoon-facing sides (back reefs) of the atoll rim (Lasagna et al. 2008, 2014). The cruise route differed slightly from year to year. In total, 172 sites were surveyed, some of them revisited over the years. The position of each site was recorded using a GPS. At each site, all data (described in more detail below) were collected by SCUBA diving at depths between 4 and 6 m.

Sea Surface Temperature (SST)

Sea surface temperature (SST) data were obtained from the US National Oceanic and Atmosphere Administration (NOAA) for the period 1997-2017 (data can be found at http://coralreefwatch.noaa.gov/vs/gauges/maldives.php) and calibrated by linear regression using discontinuous field data from our own archives (many of which were collected contemporaneously with the biological data). Two regional bleaching thresholds can be identified in the Maldives:

30.9°C for severe bleaching events that may cause widespread mortality, and 30.5°C for moderate bleaching events that have no wide-scale effects on Maldivian coral reefs (Morri et al. 2015, and references therein; NOAA 2016; Perry and Morgan 2017a). Mean and maximum SSTs were considered and compared to the known bleaching thresholds in the study area.

Data collection and management

Coral reef communities and bioconstructional guilds

Composition of reef communities was described using 17 benthic categories (Morri et al. 2010, 2015), comprised of 14 "lumped" levels of classification of sessile organisms (combining taxa with similar growth-forms) and 3 abiotic components: branching *Acropora*, digitate *Acropora*, tabular *Acropora*, branching coral, foliose coral, massive coral, encrusting coral, Fungiidae, *Tubastrea micranthus*, *Heliopora coerulea*, *Millepora*, large clam (mostly *Tridacna*), coralline algae, soft-bodied organism (i.e. soft coral, whip- and wire-coral, sea fan, fleshy algae, sponge, tunicate), dead coral/coral rock, coral rubble, and sand. For each of these benthic categories, the percent substratum cover was visually estimated by the plain view technique of Wilson et al. (2007), with divers hovering 1-2 m above the benthos over an area of about 20 m^2, in three replicate spots at each of the eight reefs at each sampling time. The observers were always the same during surveys from 1997 to 2013, while new observers trained by the former estimated cover values from 2014 to 2017.

Total hard coral cover (HCC) was obtained summing up the cover of the 11 categories of hard coral listed above. *Acropora* cover (AC) was obtained summing up the cover of the 3 categories of *Acropora*. The overall yearly means of HCC and AC were computed irrespective of reef type and site to describe the general trend of hard corals in the Maldivian reefs during the last twenty years.

To assess bioconstruction potential of a reef, five bioconstructional guilds (Fagerstrom 1991; Bianchi et al. 2017) were considered (Figure 1). The first guild is composed of primary builders, those organisms that build the reef framework and therefore assure significant reef accretion thanks to their superstratal growth; this guild was comprised of the three *Acropora* categories, branching coral, foliose coral, *Tubastrea micranthus*, *Heliopora coerulea*, and *Millepora*. The second guild includes secondary builders, which provide calcareous material to fill in the framework, and included massive coral, Fungiidae, and large clam. The third guild is made by "binders," which are encrusting coral and coralline algae that consolidate the reef structure. The fourth guild is formed by "bafflers," soft-bodied organisms that, although not actively participating in reef bioconstruction, help to retain sediment within the reef. Finally, the fifth category includes abiotic components that did not contribute to bioconstruction. Change in cover of the different bioconstructional guilds was compared over time, with a particular emphasis on the two main bleaching events (1998 and 2016). In particular, cover values were compared, in both ocean and lagoon reefs, in three distinct periods: i) pre-bleaching years: 1998 (the surveys were carried out in April, one month before the bleaching-inducing high-temperature spike) and 2015; ii) bleaching years: 1999 and 2016; and iii) post-bleaching years: 2000 and 2017.

One-way ANOVAs were performed to test for differences in substratum cover of each bioconstructional guild among pre-bleaching, bleaching and post-bleaching years over the two main bleaching events of 1998 and 2016, either in ocean or lagoon reefs. Prior to analysis, homogeneity of variances was tested by Levene's test. In the case of not homogeneous variances, ANOVA was, nevertheless, used after setting $\alpha = 0.01$ in order to compensate for the increased likelihood of Type I error (Underwood 1997). The results showing significant changes were subjected to post-hoc Tukey's test. Student t-tests, all with 22 degrees of freedom, were used to compare lagoon and ocean reef cover data in the same year, and to compare cover data in pre-bleaching, bleaching and post-bleaching years in the two reef types.

The BioConstruction Potential index BCP (Bianchi et al. 2017) was devised using equation 1:

$$BCP = \sum^{n} (s_i C_i\%) \times 100^{-1} \qquad \text{(equation 1)}$$

i=1

where n is the number of bioconstructional guilds (5, in this case), s_i is an importance score assigned to the ith guild, and C_i% is the percent cover of the ith guild. The value of s_i is 3 for the primary builders, 2 for the secondary builders, 1 for the binders, 0 for the bafflers, and -1 for the abiotic components, according to their relative role in structuring the reef framework. Therefore, BCP ranges theoretically from 3, in the unrealistic case of 100% cover by primary constructors, to -1, when only abiotic components are present and no bioconstruction is possible, the reef thus being prone to erosion and drowning.

Carbonate deposition and reef accretion

To estimate carbonate deposition rates in coral reefs, we used equation (2) proposed by Perry and Morgan (2017a):

$$CaCO_3 = 0.428\ HCC - 5.3376 \qquad \text{(equation 2)}$$

where $CaCO_3$ is the net budget of carbonate deposition in kg $CaCO_3$ m^{-2} a^{-1} and HCC is the total hard coral cover in %.

To estimate reef accretion rates we used the two equations proposed by Perry and Morgan (2017a) based on total hard coral cover (equation 3) and *Acropora* cover (equation 4):

$$PA = 0.3089HCC - 0.5827 \qquad \text{(equation 3)}$$

$$PA = 0.3089AC - 0.5827 \qquad \text{(equation 4)}$$

where PA is the reef accretion rate in mm a^{-1}, HCC and AC are the total hard coral cover and *Acropora* cover, respectively, in %.

Linear regressions were performed on a total of 480 observations to test relationships between: i) the BCP index and the net carbonate deposition rate, ii) the BCP index and the reef accretion rate considering HCC, and iii) the BCP index and the reef accretion rate considering only AC.

Diversity of constructors

The Shannon-Wiener index (H') was used to measure the diversity of bioconstructors in the reefs, applying the following equation (5):

$$H' = -\sum_{i=1}^{n} p_i \ln p_i \quad \text{(equation 5)}$$

where n is the number of categories of bioconstructors considered (13 in our case within primary builders, secondary builders, and binders); p_i is the cover (%) of the i^{th} category and ln is the natural logarithm.

Results

Sea Surface Temperature (SST)

Mean SST increased by ~ 0.25°C from 1997 to 2017. Peaks in maximum SST coincided with the known bleaching episodes that hit the Maldives during the investigated period (Figure 2a). Only the two heat anomalies of 1998 and 2016 exceeded the severe regional bleaching threshold, whilst the temperature in 2003, 2007 and 2010 exceeded only the moderate bleaching threshold and had no evident impact on the overall reef recovery pattern after the mass mortality of 1998. In 1998 the bleaching started at the beginning of May, whilst in 2016 it started in late March, and then the temperature persisted at levels above the severe bleaching threshold for nearly two months in both events.

Hard coral and Acropora *cover*

HCC, which dropped to less than 10% after the 1998 bleaching, returned to pre-bleaching values of about 55% only by 2014 (Figure 2b). The formerly dominant branching and tabular *Acropora* species completely disappeared in 1999, and recovered to nearly the half of the value of 1998 by 2014. In 2016, branching and tabular corals died once again following the new bleaching, leading to mean HCC and AC values around 20% and less than 5%, respectively. Most of the massive corals survived, showing only partial mortality. Already in 2017 reefs started to recover, reaching mean HCC values of around 30%; however, there were no evident sign of recovery for *Acropora* during our survey of May 2017.

Bioconstruction potential, carbonate deposition and reef accretion

Maldivian reefs in the pre-bleaching years (1998 and 2015) were dominated by primary builders: their cover was greater in ocean than in lagoon reefs in 1998 ($t = -9.55$, $p<0.001$) but exhibited no difference in 2015 ($t = 0.59$, $p = 0.59$) (Figure 3). In ocean reefs, primary builders showed higher cover in 1998 than in 2015 ($t = 3.12$, $p < 0.01$). Cover of binders was significantly lower in ocean compared to lagoon reefs in 1998 ($t = 35.1$, $p < 0.001$), but similar in both reef systems in 2015 ($t = 0.93$, $p = 0.36$). Both in lagoon and ocean reefs binders were more abundant in 2015 than in 1998 ($t = -2.33$, $p<0.05$; $t = -5.05$, $p<0.001$, respectively). In 1998, there were almost no abiotic components on ocean reefs, while covering over 20% in lagoon reefs ($t = 22.3$, $p<0.001$). In 2015, abiotic cover in ocean reefs increased significantly ($t = -3.48$, $p<0.01$) and was similar to the cover in lagoon reefs. In general, the difference between ocean and lagoon reefs was much more pronounced in 1998 than in 2015.

In the aftermath of the two bleaching episodes, reefs were dominated by abiotic components, which showed higher cover in ocean reefs compared to lagoon reefs after the 1998 bleaching event ($t = -7.10$, $p<0.001$ in 1999; $t = -8.69$, $p<0.001$ in 2000), but much higher in lagoon reefs after the 2016 bleaching ($t = 4.32$, $p<0.001$). Following the bleaching 1998, primary builders almost disappeared in 1999 in both reef types (Table 1a), but were significantly higher in lagoon compared to ocean reefs ($t = 7.74$, $p<0.001$). In 2016, their cover in both reef systems declined significantly to <20% (Table 1b). Secondary builders halved their cover during both events in ocean reefs, whilst no change in cover was detected in lagoon reefs during both bleaching events (Table 1a, b). Binders declined in 1999 in lagoon reefs (Table 1a) and disappeared in 2016 in both reef types (Table 1b).

Bafflers increased their cover values in lagoon reefs in 1999 (Table 1a), showing higher cover than in ocean reefs ($t = 6.12$, $p<0.001$), whilst no change in cover was detected in both ocean and lagoon reefs in the second bleaching event (Table 1b).

The post-bleaching reef composition showed different trends following the 1998 and 2016 bleaching events. After 1998, there was a significant recovery of binders in both the lagoon and ocean reefs already by 2000 (Table 1a), where they reached higher cover compared to ocean reefs ($t = 32.16$; $p < 0.001$). After the 2016 bleaching, primary builders in lagoon reefs continued to decline significantly (Table 1b) and showed cover values lower than in ocean reefs ($t = -1.87$; $p < 0.05$), while decreasing only slightly in ocean reefs and staying above the 2000 post-bleaching values ($t = -2.6$; $p < 0.01$) (Figure 3). Cover of secondary builders and binders recovered to pre-bleaching values by 2017 in ocean reefs (Table 1b) and became the dominant reef builders, especially in the ocean reefs ($t = 3.54$, $p<0.01$; $t = -2.65$, $p<0.05$, respectively).

The BCP was positively and highly correlated with both carbonate deposition rate and reef accretion rate considering total HCC, with extremely small error terms; correlation was slightly lower, and error terms larger, for AC-only accretion rate (Figure 4).

After the bleaching event of 1998, all shallow reefs exhibited net erosion, i.e., negative BCP values (Figure 5). It took two years for the lagoon reefs and three years for the ocean reefs to re-initiate positive carbonate deposition, and this was mainly due to binders and bafflers that retained sediments; the few primary and secondary builders could not yet ensure positive bioconstruction. Attainment of constratal growth (BCP between 0 and 1) required six years (lagoon reefs) or nine years (ocean reefs). However, BCP values lower than 1 indicate reefs with few primary builders. Values of BCP greater than 1 (corresponding to hard coral cover >50% in the Maldives), are indicative of superstratal growth due to the relatively high cover of primary builders. Maldivian reefs attained BCP > 1 in 1997-1998 and again after 2012 (lagoon reefs) or 2014 (ocean reefs), fourteen to sixteen years after the first severe bleaching event, respectively. During the bleaching episode of 2016, both lagoon and ocean reefs fell to negative BCP values indicative of no bioconstruction, but a low level of carbonate deposition by binders and bafflers restrained erosion. In 2017 BCP declined further in lagoon reefs, leading to a net erosive budget, whereas ocean reefs resumed constratal growth.

These changes in carbonate deposition have driven major reductions in reef growth during both severe bleaching events. In the pre-bleaching years (1998 and 2015), reef accretion of Maldivian reefs ranged between 12.1 and 18.9 mm a^{-1} depending on reef type (Figure 5). After the 1998 bleaching, accretion of reefs was null and then started slowly to recover in the following years. During the 2016 event, reef accretion declined to values lower than 3.6 mm a^{-1}; in the post-bleaching year it showed some recovery in ocean reefs, while values in lagoon reefs continued to decline.

Diversity of the constructors

Diversity of the bioconstructors showed different temporal trajectories comparing lagoon and ocean reefs. In the lagoon reefs, the two severe bleaching events followed similar trajectories, with four distinct phases (Figure 6): i) decline in bioconstructor diversity in pre-bleaching years (1997-1998 and 2014-2015), probably due to early mortality through thermal stress before mass bleaching became evident; ii) sudden and dramatic reduction in BCP, with no further reduction in diversity, in the bleaching years; iii) increase in bioconstructor diversity in the post-bleaching years; iv) gradual increase in BCP. In the ocean reefs, the four phases were not equally obvious, and trajectories of change differed in response to the two bleaching events.

Discussion

Among the three pan-tropical global bleaching episodes (Heron et al. 2016) only those of 1997-1998 and 2015-2016 caused high mortality on coral reefs in the Maldives, whilst the bleaching of 2010 had only minor consequences (Guest et al. 2012). The dominant *Acropora* corals nearly disappeared during both 1998 and 2016, as they are typically highly susceptible to thermal stress (Loya et al. 2001; Baker et al. 2008; Guest et al. 2012; Pratchett et al. 2013). On the contrary, massive corals experienced mostly partial colony mortality (Bianchi et al. 2003), as similarly observed in other Maldivian atolls (Perry and Morgan 2017b) and in the nearby Chagos Archipelago (Sheppard et al. 2008, 2017).

Total hard coral cover is the most commonly used indicator of reef health but may not be a sufficient predictor of reef growth potential (Lasagna et al. 2010a, and references therein). The BCP index (Bianchi et al. 2017), which is based on cover values of bioconstructional guilds, illustrates shifts from superstratal to constratal accretion and to erosive state. Integrating the BCP index with the equations developed by Perry and Morgan (2017a) allowed transforming our cover data into a proxy for carbonate deposition and reef accretion. Superstratal growth in the Maldives was normally assured by the canopy of large and fast-growing *Acropora* corals (Morri et al. 1995; Lasagna et al. 2010b). Contrarily to what observed by Perry and Morgan (2017a), *Acropora* cover did not result a strong predictor of reef accretion in our study. Thus, we used total hard coral cover (which anyway also includes *Acropora* corals) to estimate reef accretion through the predictive equation of Perry and Morgan (2017a).

After both mass bleaching events, all lagoon and most of the ocean Maldivian reefs shifted from a net accretion to a net erosive state. After the 1998 bleaching event, the coral communities took around 16 years to recover the constructional capacity of the pre-bleaching year (Pisapia et al. 2016; Bianchi et al. 2017). Recovery started with a low coral carbonate production that maintained reefs in a long phase of virtually no bioconstruction (from 5 to 9 years in lagoon and ocean reefs, respectively); recovery then passed through a period of constratal accretion, in which the reef grew at a rate of about 3.6-9.5 mm a^{-1}, after which high accretion rates resulted in the return to the original 3D-structure in all reefs. The new severe bleaching event of 2016 pushed Maldivian reefs into a no bioconstruction state once again. In the Great Barrier Reef, past exposure to bleaching in 1998 did not lessen the severity of bleaching in 2016 (Hughes et al. 2017b), whereas in the Maldives, mortality rate in 2016 was lower than in 1998. Our data suggested that after both events high diversity of constructors was an essential trigger for enhancing bioconstruction, as underlined by previous studies elsewhere (Benzoni et al. 2003; van Woesik, 2017), but lagoon and ocean reefs showed inconsistent temporal trends of the relationship between BCP and diversity (Figure 6). Lagoon reefs had a predictable and consistent pattern during and after both bleaching events, with a four-phase cycle that resembles the adaptive cycle described by Holling (2001). In both ocean and lagoon reefs, a higher spatial variability in bioconstructor diversity was apparent in 2015, at the beginning of the last bleaching event, and might be interpreted as an early symptom of stress (Warwick and Clarke 1993).

Bleaching is likely to become a chronic stressor in the coming decades (Hughes et al. 2018), implying repeated coral mortality, reduced reef accretion and risk of drowning following sea level rise (Perry et al. 2018). In the Maldives, constratal accretion, regained 6-9 years after the severe bleaching of 1998, seems enough for reefs to keep-up with the ongoing yearly mean sea level rise of 2 mm. According to the Intergovernmental Panel on Climate Change (IPCC 2013), such a rate of sea level rise can be maintained under the most optimistic scenario (Heron et al. 2017), corresponding to low carbon dioxide (CO_2) emissions and a Representative Concentration Pathways RCP = 2.6 (van Vuuren et al. 2011). However, sea surface temperature increase is likely to exceed coral tolerance limits in the next decades (Heron et al. 2017). Models suggest that the majority of coral reefs will not survive the most pessimistic scenarios predicted for global warming (Frieler et al. 2013; Perry et al. 2018). The worst IPCC scenario envisages 10 mm a^{-1} of sea level rise (Heron et al. 2017) with a RCP = 8.5 (IPCC 2014); expert judgement by several scientists underlines model uncertainty, leading to an even more pessimistic, but precautionary, prediction of a mean yearly sea level rise of 20 mm (Melillo et al. 2014). A foreseen global temperature increase of up to 5-6 ºC by the year 2100 (https://sos.noaa.gov/Datasets/dataset.php?id=438) would cause two severe bleaching events per decade (Hughes et al. 2018), a frequency that prevents recovery of Maldivian coral reefs (Table 2). Under this scenario, more than 80% of coral reefs will be degraded by 2040 (Heron et al. 2017): Maldivian reefs will not have sufficient time to recover prior to the next severe bleaching and will therefore experience drowning and extinction of stenothermal species (Bay et al. 2017). Large-scale bleaching two years in a row have already been documented for the first time in 2014-2015 in Hawaii and in the Florida Keys, and in 2016-2017 on the Great Barrier Reef (Warner et al. 2016). To cope with 20 mm annual sea level rise, coral reefs would have to reach a BCP value of 3, which would be gained only with the rather unrealistic situation of 100 % cover of primary builders.

The COP21 Paris agreement set the goal of holding the increase in the global average mean temperature to well below 2 °C above preindustrial levels, but called for efforts to limit that increase to 1.5 °C (UNFCCC 2015). Even with this optimistic assumption of warming, two-thirds of reefs worldwide will disappear (Frieler et al. 2013). Climate-related loss of reef ecosystem services will total US$ 500 billion per year or more by 2100, with the greatest impacts felt by people who rely on reefs for their daily subsistence (Heron et al. 2017). Local anthropogenic impacts may exacerbate the effects of climate change (Nepote et al. 2016; Brown et al. 2017; Prouty et al. 2017). Reducing local threats to corals could make coral reef ecosystems more resilient to rising ocean temperatures and help reducing coral reef decline globally (Sheppard et al. 2017; Shaver et al. 2018), favouring high recruitment and recruit survival rates (Cardini et al. 2012; Shlesinger and Loya 2016). Long-term series of data remain the most effective tool to validate predictive models and evaluate temporal patterns, and should be a priority for reef scientists and managers alike (Bianchi et al. 2017; Osborne et al. 2017). Attention should be focused on the preservation of bioconstructional capacity to ensure continued accretion of coral reefs: our BioConstruction Potential index would be of help in this respect.

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Figure captions and Table headings

Figure 1. The five bioconstructional guilds considered in the present study, with some examples of benthic categories for each guild: a) primary builders, including tabular *Acropora* (i), coral branching (ii), and *Tubastrea micranthus* (iii); b) secondary builders, including massive coral (i), Fungiidae (ii), and large clam such as *Tridacna* (iii); c) binders, which include encrusting coral (i, ii) and coralline algae (iii); d) bafflers, including soft-coral (i), sea fan (ii) and erect sponge (iii); e) abiotic components such as dead coral/coral rock (i), coral rubble (ii), and sand (iii).

Figure 2. Twenty-year trends (1997-2017) of sea surface temperature (SST) and percentage cover of hard corals in the Maldives. a) Yearly maximum (red continuous line) and mean (dotted black line) SST. Sun icons indicate years with known bleaching episodes for the study area, distinguished in moderate (i.e., causing little mortality) and severe (i.e., causing mass mortality) events (from Morri et al. 2015 and references therein; NOAA 2016). The threshold temperatures triggering moderate and severe bleaching events are also reported (according to Perry and Morgan, 2017a and present data). b) Mean (± standard error) hard coral (HCC) and *Acropora* (AC) cover (in %) in the Maldives. Bold values on the x axis correspond to years when bleaching events have been reported for the Maldives.

Figure 3. Mean (+ standard error) percent substratum cover (%) of primary builders, secondary builders, binders, bafflers, and abiotic components in lagoon and ocean reefs over the two severe bleaching events: 1998 (top row) and 2016 (bottom row). For the former bleaching event, which began in May of 1998, data from the year 1998 collected in April were considered as pre-bleaching values, data from 1999 as during-bleaching, and data from 2000 as post-bleaching. For the latter bleaching event, data from 2015 and 2017 are considered as pre- and post-bleaching values,

respectively. Differences between lagoon and ocean reefs were tested using student t-tests (* = $p<0.01$, ** = $p<0.001$).

Figure 4. Linear regressions showing the relationships between: a) BioConstruction Potential index (BCP) and net carbonate deposition rate (kg $CaCO_3$ m^{-2} a^{-1}); b) BCP and reef accretion rate (mm a^{-1}) considering total hard coral cover (HCC); c) BCP and reef accretion rate (mm a^{-1}) considering *Acropora* cover (AC) only. Equations of the models and R^2 values are reported. The 95% bootstrapped confidence intervals are represented by the grey zones in all panels.

Figure 5: Trend of the mean values (± standard error) of BioConstruction Potential index (BCP), on shallow (4-6 m) lagoon and ocean reefs in the Maldives, 1997-2017. Negative values of BCP imply no bioconstruction, values between 0 and 1 depict reefs capable of constratal growth only, values greater than 1 are indicative of superstratal growth (see text). Values of reef accretion (mm a^{-1}) are indicated in correspondence with each threshold of the BCP. The threshold to pass from a net positive to a net negative carbonate budget (in term of $CaCO_3$ deposition) and the threshold of the null accretion are also reported, which correspond to reefs prone to erosion. Bold values on the x axis correspond to years when bleaching events have been reported for the Maldives.

Figure 6. Diagrams showing values of BioConstruction Potential index (BCP) and diversity of bioconstructors (expressed by the Shannon-Wiener index H' applied to 13 bioconstructor categories) in lagoon and ocean reefs from 1997 to 2017. Smaller numbers are individual replicates, bold numbers are year centroids. Recovery patterns from the two severe bleaching events are illustrated by the time trajectories of year centroids in the periods 1997-2013 (light purple) and 2014-2017 (dark pink).

Table 1. Results of 1-way ANOVAs on the five bioconstructional guilds among the three years of the first severe bleaching event (a; 1998, 1999, and 2000) and the second severe bleaching event (b; 2015, 2016, and 2017), in lagoon and ocean reefs. Significant values are in bold, * = $p < 0.01$; ** = $p < 0.001$.

Table 2. Maldivian reef status under different predicted scenarios of yearly sea level rise and bleaching frequencies; bad status may imply reef drowning. [1] = the optimistic scenario, which predicts a yearly mean sea level rise of 2 mm, corresponds to a Representative Concentration Pathways RCP = 2.6 (IPCC, 2013); the IPCC worst scenario, which predicts 10 mm a^{-1} of sea level rise, corresponds to RCP = 8.5 (IPCC, 2013); the most pessimistic and precautionary scenario predicts a mean yearly sea level rise of 20 mm (Melillo et al. 2014). [2] = predicted bleaching frequencies in the best scenario (every 15 years), intermediate scenario (every 10 years), and worst scenario, where a bleaching event every 5 years is expected (Heron et al. 2017).

Table 1.

a)		**Primary builders**		**Secondary builders**		**Binders**		**Bafflers**		**Abiotic components**	
LAGOON	df	SS	p	SS	p	SS	p	SS	p	SS	p
Between groups	2	18185.1	**<0.001**	35.389	0.012	1314.06	**<0.001**	725.056	**<0.001**	16368.2	**<0.001**
Within groups	33	193.25		116.167		34.25		124.5		414	
Total	35	18378.3		151.556		1348.31		849.556		16782.2	
Levene's test		p<0.001		p<0.001		p=0.689		p<0.001		p=0.036	
Tukey's pairwise		1998>1999**				1998>1999**		1998<1999**		1998<1999**	
		1998>2000**				1998<2000**		1999>2000**		1998<2000**	
						1999<2000**				1999>2000**	
OCEAN	df	SS	p	SS	p	SS	p	SS	p	SS	p
Between groups	2	40422.7	**<0.001**	2525.17	**<0.001**	106.167	**<0.001**	219.556	**0.004**	54014.1	**<0.001**
Within groups	33	499.51		835.583		20.583		565.667		127.583	
Total	35	40922.2		3360.75		126.75		785.222		54141.6	
Levene's test		p<0.001		p<0.001		p=0.492		p<0.01		p<0.001	
Tukey's pairwise		1998>1999**		1998>1999**		1998<1999*		1998<2000**		1998<1999**	
		1998>2000**		1998>2000**		1998<2000**				1998<2000**	
						1999<2000**				1999>2000**	

b)		**Primary builders**		**Secondary builders**		**Binders**		**Bafflers**		**Abiotic components**	
LAGOON	df	SS	p	SS	p	SS	p	SS	p	SS	p
Between groups	2	13436.2	**<0.001**	22.722	0.848	1905.56	**<0.001**	92.389	0.457	23521.7	**<0.001**
Within groups	33	5883.33		2254.83		1836.33		1900.5		6848.5	
Total	35	19319.6		2277.56		3741.89		1992.89		30370.2	
Levene's test		p<0.01		p=0.173		p<0.001		p=0.593		p=0.118	
Tukey's pairwise		2015>2016**				2015>2016**				2015<2016**	
		2015>2017**				2015>2017*				2015<2017**	
		2016>2017*									
OCEAN	df	SS	p	SS	p	SS	p	SS	p	SS	p
Between groups	2	6274.06	**0.002**	3856.06	**0.004**	1458	**<0.001**	228.389	0.076	15251.7	**<0.001**
Within groups	33	13974.5		9707.5		1735		1353.25		9912.17	
Total	35	20248.6		13563.6		3193		1581.64		25163.9	
Levene's test		p<0.001		p<0.01		p<0.001		p=0.019		p=0.314	
Tukey's pairwise		2015>2016**		2015>2016*		2015>2016**				2015<2016**	
		2015>2017**		2016<2017*		2016<2017**				2015<2017*	
										2016>2017*	

Table 2.

		yearly sea level rise[1]		
		2 mm	10 mm	20 mm
bleaching frequency[2]	15 years	GOOD	QUESTIONABLE	BAD
	10 years	GOOD	BAD	BAD
	5 years	QUESTIONABLE	BAD	BAD

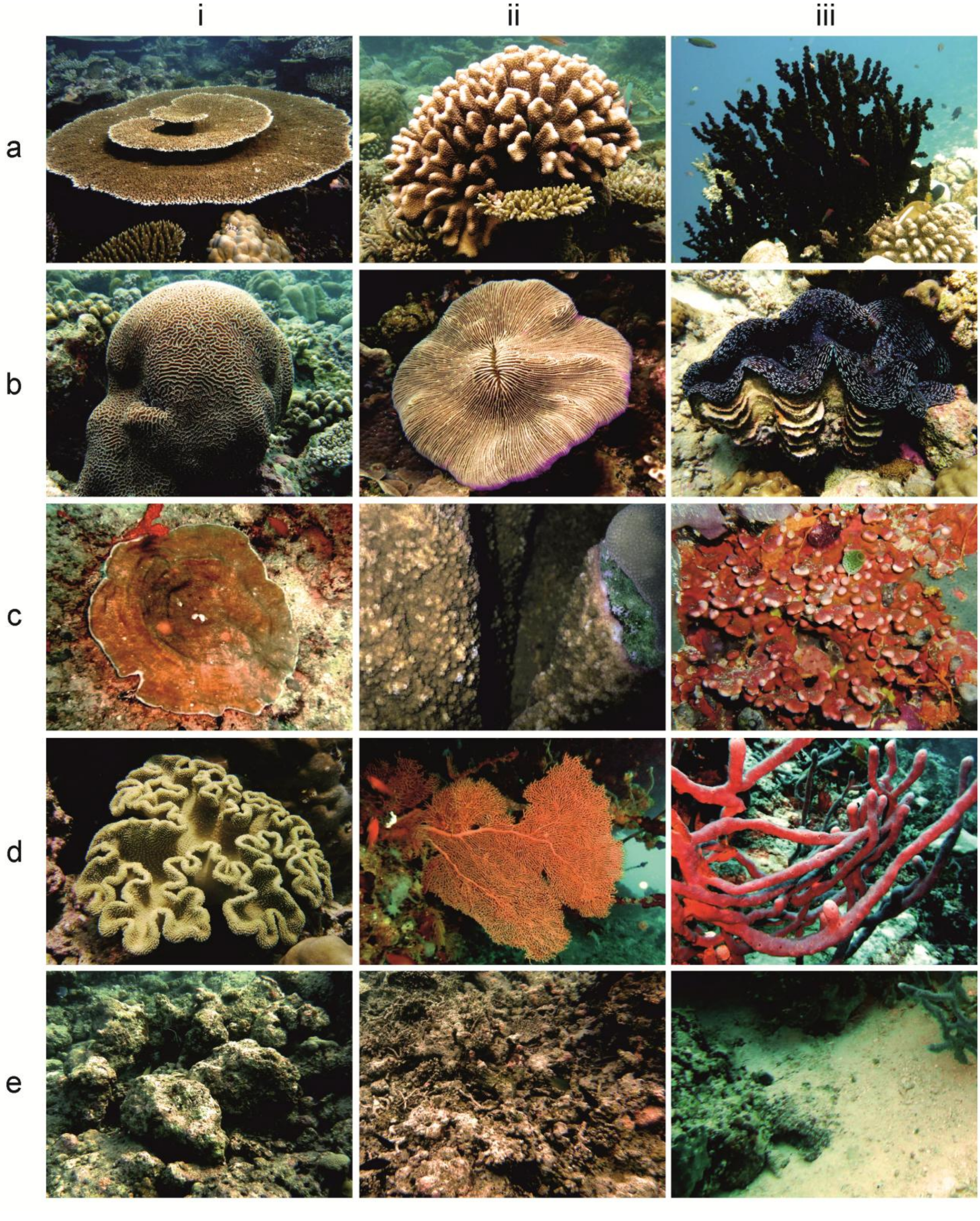


Figure 1

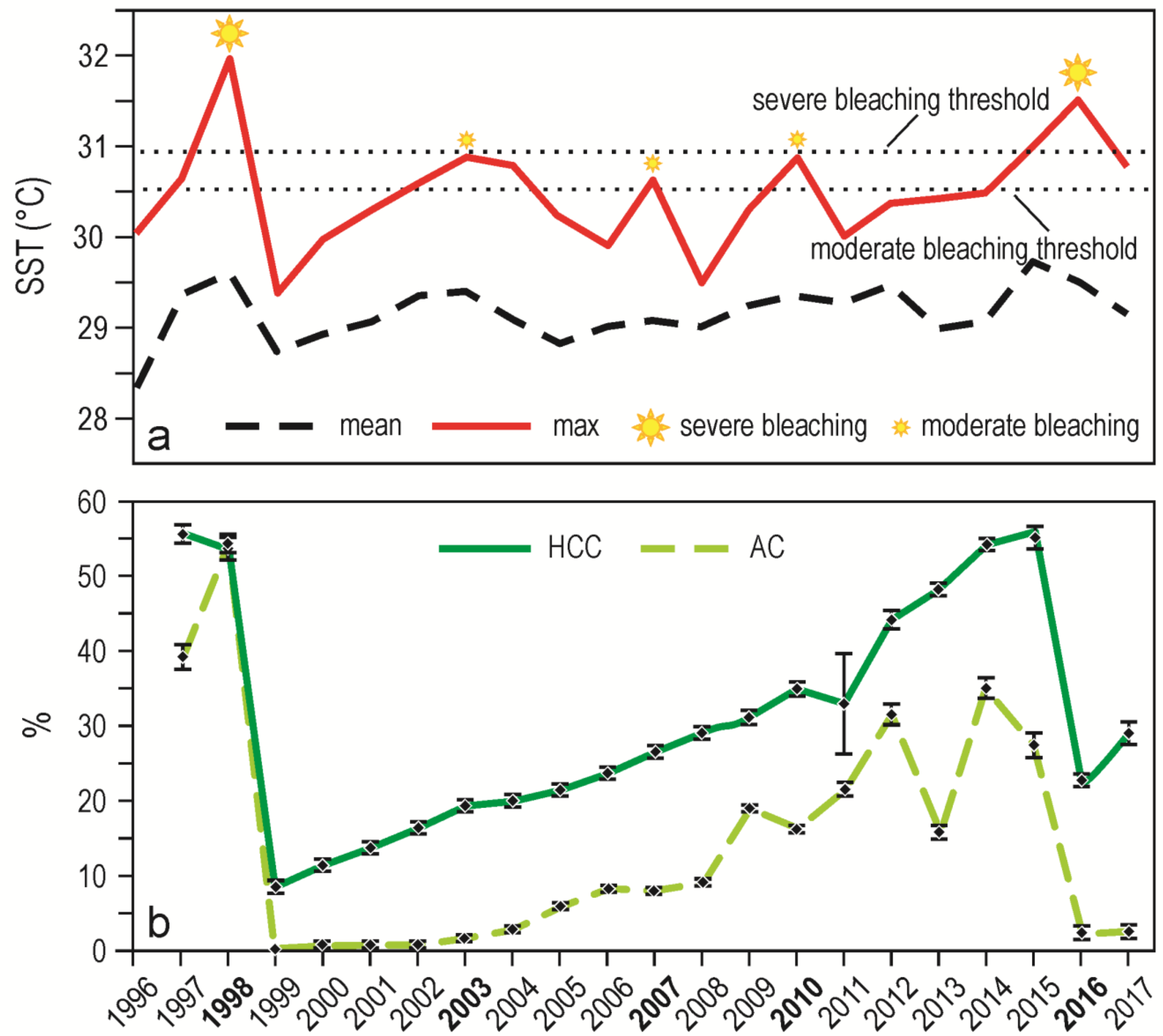

SST (°C)
32
31
30
29
28
severe bleaching threshold
moderate bleaching threshold
a
mean
max
severe bleaching
moderate bleaching
60
50
40
30
20
10
0
%
HCC
AC
b
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017

Figure 2

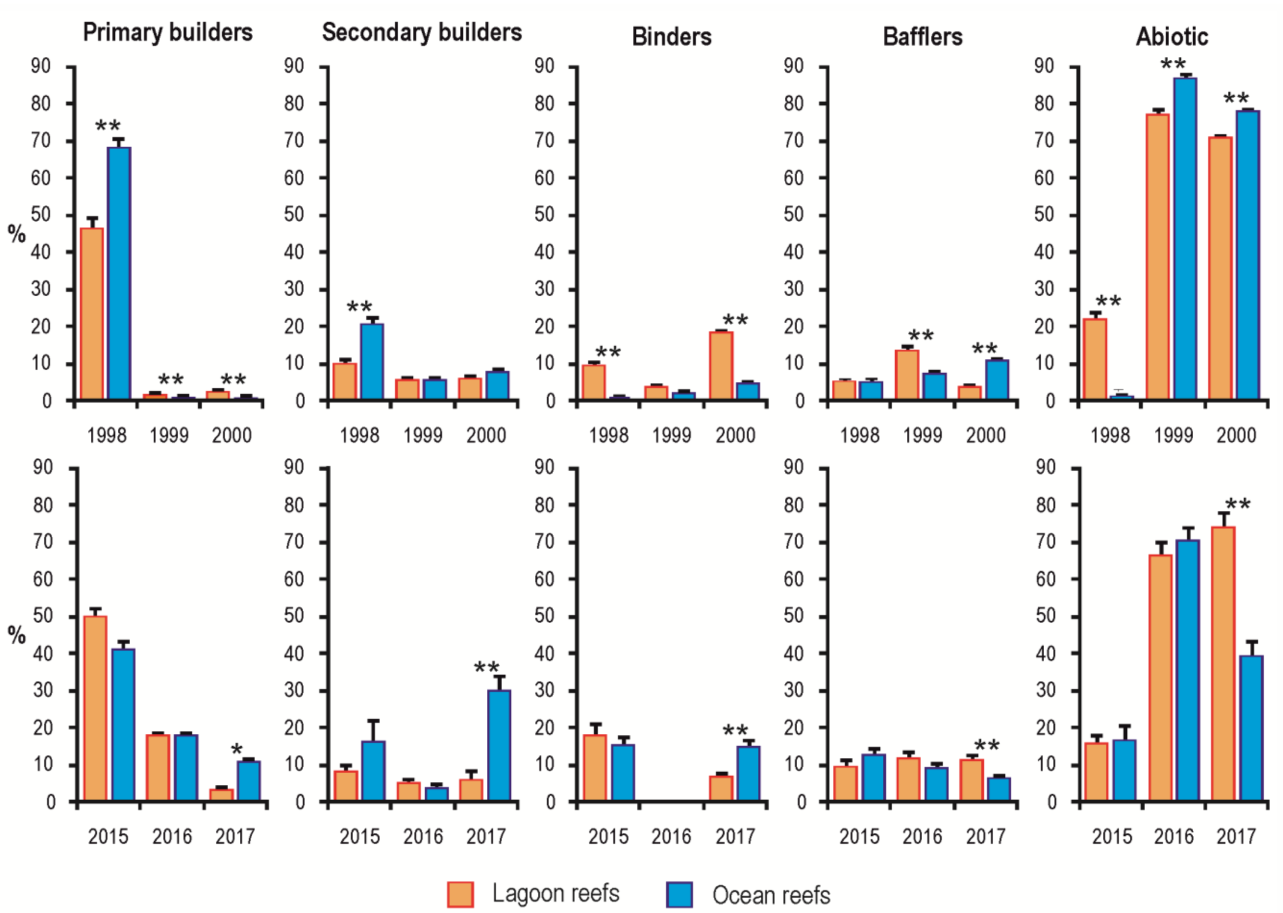


Figure 3

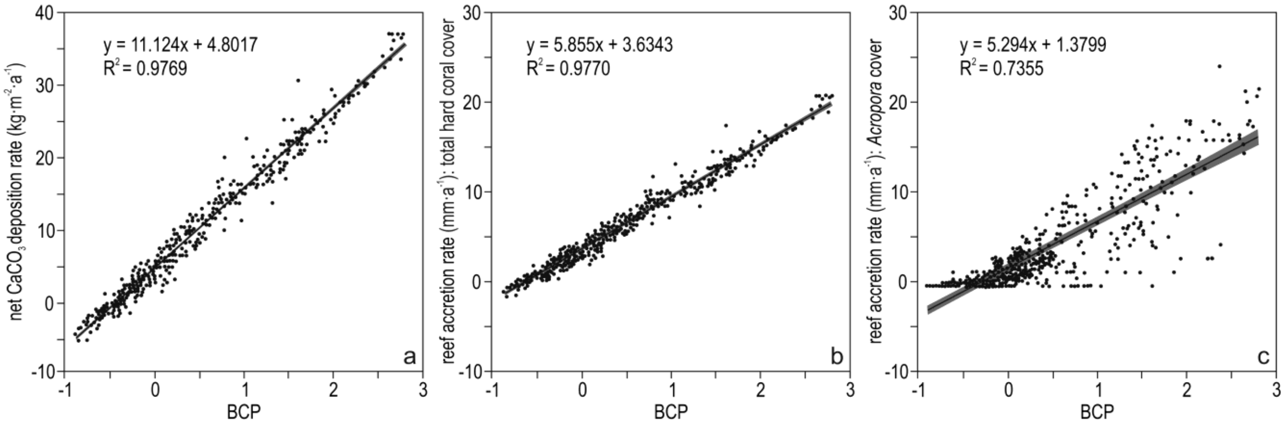
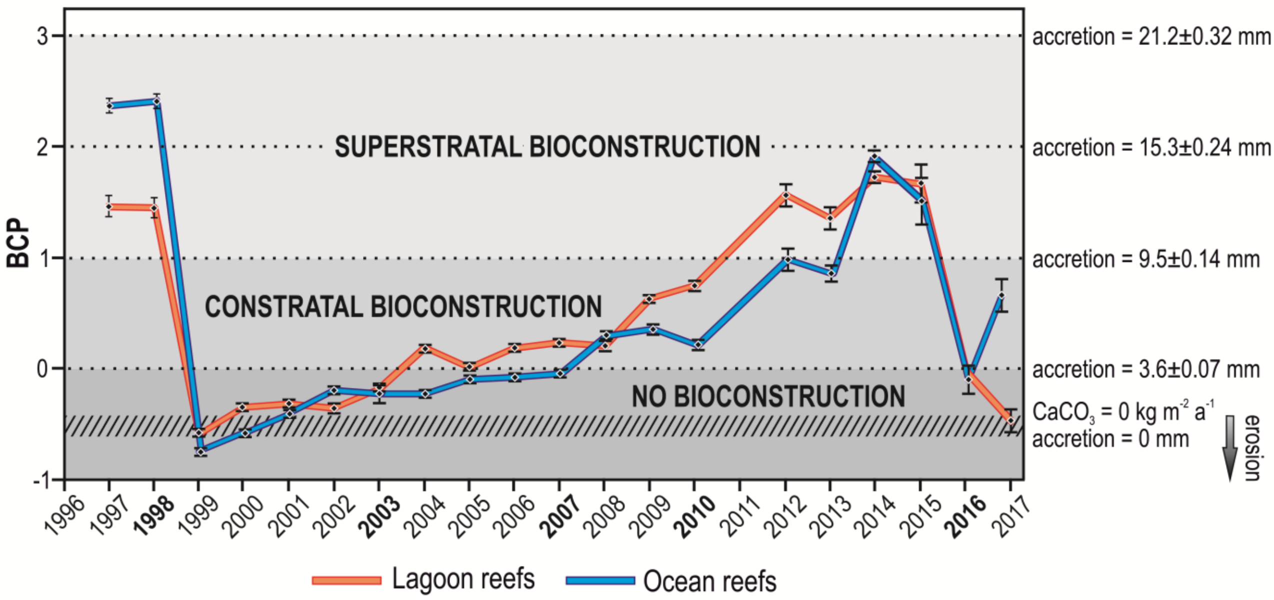


Figure 4



BCP
SUPERSTRATAL BIOCONSTRUCTION
CONSTRATAL BIOCONSTRUCTION
NO BIOCONSTRUCTION
accretion = 21.2±0.32 mm
accretion = 15.3±0.24 mm
accretion = 9.5±0.14 mm
accretion = 3.6±0.07 mm
CaCO3 = 0 kg m-2 a-1
accretion = 0 mm
erosion
1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017
Lagoon reefs
Ocean reefs

Figure 5

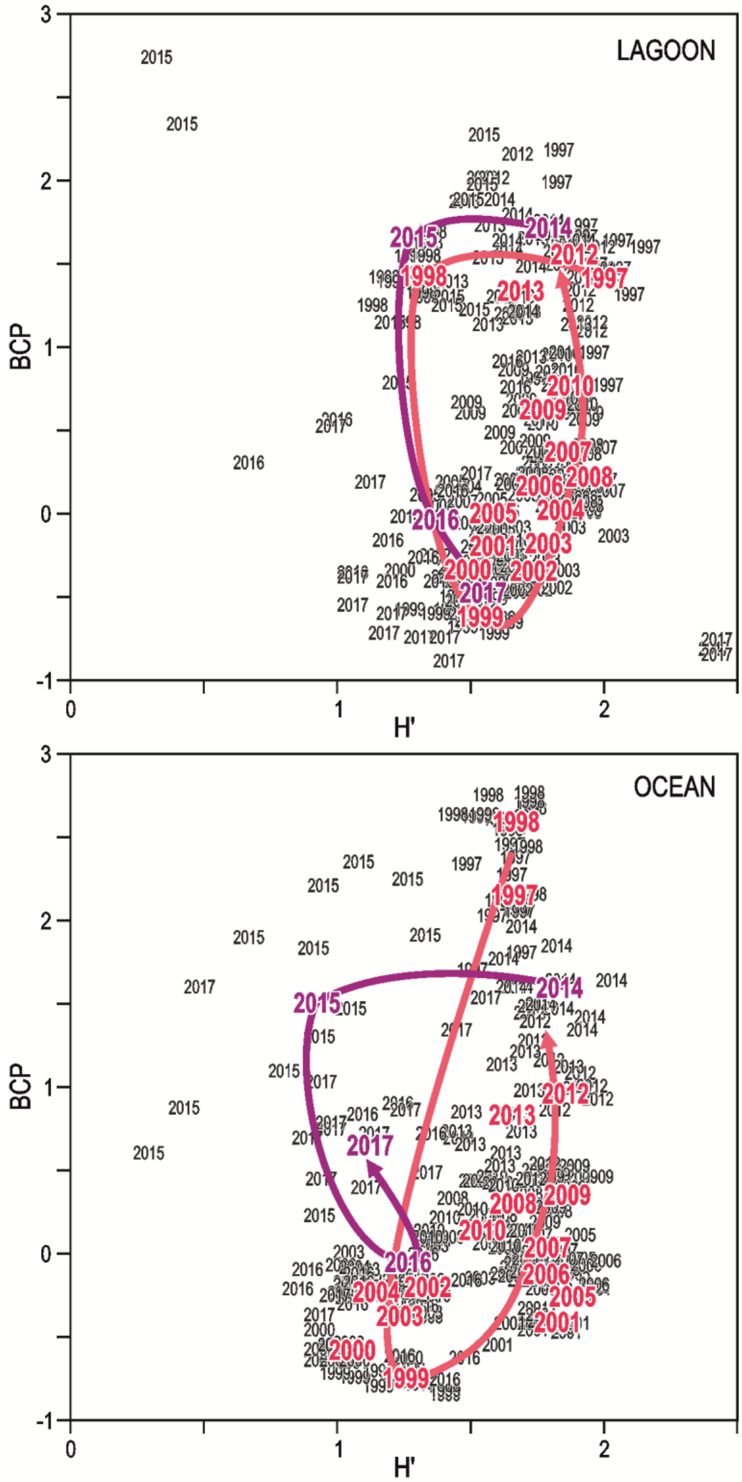


Figure 6